The Vertebral Column and Appendicular Skeleton of *Leiopelma hochstetteri* Fitzinger

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Introduction

The limb girdles and abdominal ribs of various species of *Leiopelma* have been described or figured by McCulloch (1919), Noble (1931) and de Vos (1938 A and B) but a complete description of the skeleton of this important and primitive frog has not previously been published. In the following account, which is based primarily on a study of *Leiopelma hochstetteri* Fitzinger, the skeleton as a whole is described and reference is made to variations encountered when dealing with several rather than single specimens. The vertebral column and the carpus and tarsus of *Leiopelma* are here described for the first time. As far as possible comparison has been made with *Ascaphus truei,* the only other member of the Leiopelmatidae (Liopelmidae, Noble, 1924).*

Techniques Used in Skeletal Study

(a) Alizarin transparencies of whole animals.
(b) Differential staining of cartilage and bone by the method of Williams (1940).
(c) X-ray photographs.
(d) Dried and disarticulated bones, especially vertebrae.
(e) Serial sections through various regions.

Where microscopical study was considered necessary, contour reconstructions were made using the method described by Pusey (1939).

Acknowledgments

To my supervisor at University College, London, Professor D. M. S. Watson, F.R.S , I am deeply grateful for advice and encouragement. My thanks are also due to the following: The Minister of Internal Affairs, Wellington, for permission to collect and export specimens of *Leiopelma;* Mr. E. G. Turbott, M.Sc., of the Auckland War Memorial Museum, for the loan of two adult specimens of *Ascaphus truei,* the X-ray photographs of which have been extremely useful; Dr. W. Wallace Main and Mr. B. N. Gibson, of Auckland, and Mr. Venning, of the Department of Anatomy, University College, London, who prepared X-ray negatives for me; Mr. W. A. Brackenbury, of the

* By permission of the Department of Internal Affairs, Wellington, I was allowed to export a certain number of specimens of *Leiopelma* to London for use in research. A description of the skeleton of some of these frogs formed an appendix to a thesis presented for the degree of Doctor of Philosophy in the University of London and is the basis of this paper. It must be noted, however, that an outline description of the skeleton of *Leiopelma* is to be found in a thesis lodged in the library of Auckland University College (Turbott, 1937). I had not seen this account until very recently and my own observations were made quite independently.

Vol. 79, Parts 3–4, pp. 601–613, Plates 130–131, 7 figs. March, 1952

Department of Zoology, University College, London, for a photograph of the vertebral column.

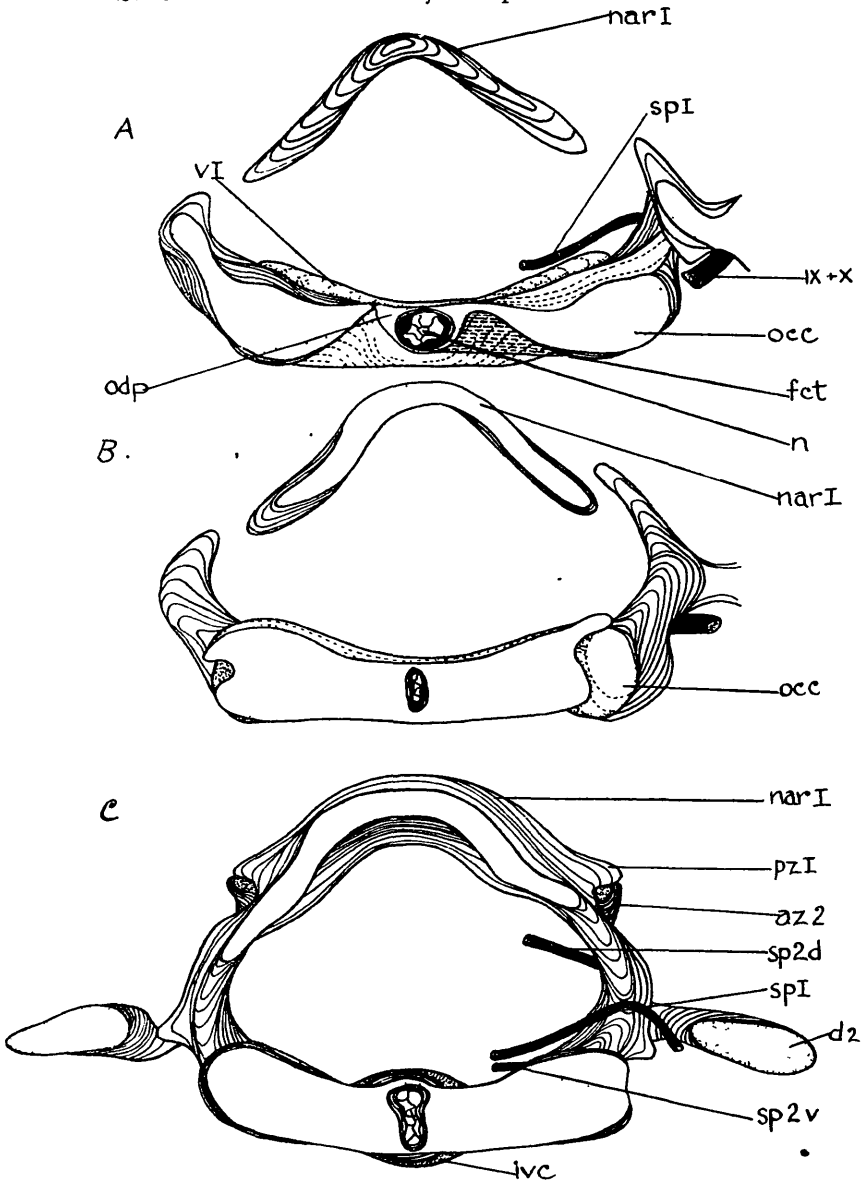
THE VERTEBRAL COLUMN (Plates 130 and 131)

Leiopelma shares with *Ascaphus* the distinction of having nine presacral vertebrae, one more than any other Anuran. The vertebrae of these two genera are also unique among frogs and toads through the fact that each is amphicoelous, the centrum being biconcave and the intervertebral cartilage undivided. As McBride (1931) has pointed out in connection with the urodeles *Amphiuma* and *Menobranchus*, the term "amphicoelous" used for these amphibians is not strictly the same as in the herring, where the notochord is expanded between successive vertebrae. In Amphibia having biconcave centra, cartilaginous intervertebral pads are present uniting successive vertebrae, while the original notochord running through the intervertebral region becomes crushed and virtually obliterated.

Neural spines are not sharply defined on any of the vertebrae. The two facets on the "atlas" for the articulations of the occipital condyles are oval and relatively shallow (Plate 131, fig 1). Ventrally, a process of which the most anterior portion remains cartilaginous, projects forward between the occipital condyles, the space between its tapering extremity and the condyles being filled with fibrous connective tissue (Text-fig. 1A). This anterior process does not appear to be identical with the odontoid process of urodeles.

The atlas vertebra of *Leiopelma* has no transverse processes. Noble's drawing of the atlas of *Ascaphus* (Noble, 1931, p. 488) shows a small but unmistakable pair of forwardly directed diapophyses. I have examined X-ray photographs of a male and female *Ascaphus*, however, and found no trace of these structures. Furthermore, it should be noted that the fossil form *Protobatrachus* (Piveteau, 1937) lacks transverse processes on the first vertebra.

The transverse processes of the vertebra next behind the atlas, the first of the thoraco-lumbar series, are usually fairly short and are directed slightly forward The third and fourth vertebrae (second and third in trunk region) invariably bear ribs which have constant and characteristic shapes (Plate 130, fig. 1). The possession of ribs in certain members of the Anura is undoubtedly a primitive feature, although the ribs themselves may show certain specialisations. Only *Leiopelma*, *Ascaphus* and the Discoglossidae bear ribs in the adult. Members of the Pipidae possess them in larval stages, but in adult life the ribs become indistinguishably fused with the diapophyses (Noble, 1931). Mookerjee (1936) has found ribs in the embryos of *Rana temporaria* and *Bufo melanostictus*. In *Leiopelma* each rib is approximately the same length as the diapophysis with which it articulates, is somewhat flattened distally, and is narrowest at the middle of its length. Distally each rib divides to form a process which is characteristic for the vertebra to which the rib belongs. The rib attached to the third vertebra has a narrow, sharp, posteriorly directed uncinate process, while that of the fourth vertebra usually ends in two more or less equal flattened expansions. Both of these ribs and their processes agree quite closely with those of *Ascaphus* (Noble, 1931)



TEXT-FIG. 1—Contour Reconstructions of Anterior Vertebral Region of *L. hochstetteri*, approximately one year old.

A. Cranio-occipital joint, anterior view. The most anterior section passes through the occipital condyles.

B. Cranio-occipital joint, posterior view. The most posterior section passes through the atlas vertebra.

C. Part of atlas vertebra and the most anterior region of the second vertebra, anterior view.

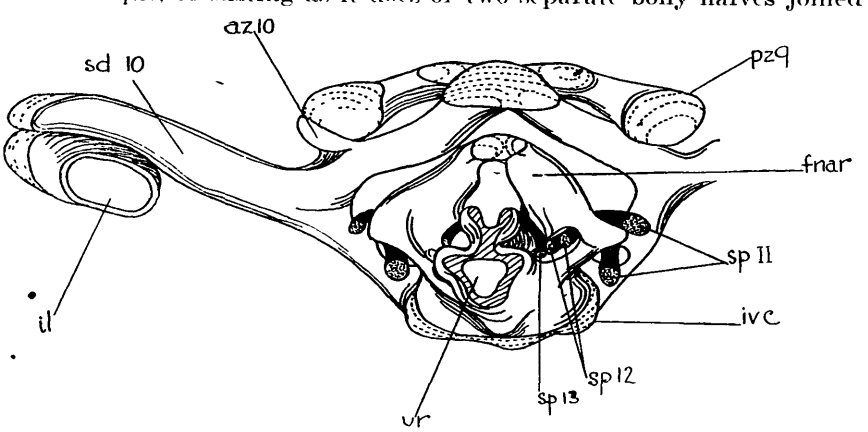
az2, anterior zgyapophysis of second vertebra; d2, diapophysis of second vertebra; fct, fibrous connective tissue; ivc, intervertebral cartilage; n, notochord; narI, neural arch of first vertebra; occ, occipital condyle; odp, anterior process; pzI, posterior zygapophysis of first vertebra; spI, first spinal nerve; sp2d, dorsal root of second spinal nerve; sp2v, ventral root of second spinal nerve; ur, urostyle; vI, atlas vertebra; IX+X, combined ninth and tenth cranial nerves

except that the more posterior rib of *Leiopelma* is developed equally as well if not better than that of the third vertebra.

Piveteau's interesting comparison (*op. cit.*) between the anterior vertebrae of *Protobatrachus* and *Ascaphus* can equally well include those of *Leiopelma*. In all three genera the rib belonging to the third vertebra articulates by a single head with the corresponding transverse process, so that in all three cases specialisation has occurred in comparison with the double-headed ribs of Amphibia such as *Miobatrachus* (Watson, 1939). The rib bears an uncinate process of uniform type. Piveteau pointed out that the enlarged size of this rib in *Protobatrachus* was repeated in *Ascaphus* and that in *Rana* also the transverse diapophysis of the third vertebra was greater than the rest. He regarded the phenomenon as being correlated with the presence of lymph hearts immediately behind the third vertebra. In view of Piveteau's explanation it is interesting to find that in *Leiopelma* no distinction occurs between the relative development of the diapophyses and ribs of the third vertebra and those of the fourth. In *Leiopelma* also it is by no means rare to find a third rib or pair of ribs attached to the fifth vertebra (Plate 130, fig. 1). When these occur, they bear no processes and are approximately the same diameter as the corresponding transverse processes.

The transverse processes of the third, fourth, fifth and sixth vertebrae point either straight out or slightly backwards (Plates 130 and 131). Those of the seventh and eighth turn slightly forward, while those of the ninth usually have a markedly forward position (Plate 130, fig. 1; Plate 131, fig. 7). The post-zygapophyses of the ninth vertebra are usually enlarged compared with those of the rest of the series (Plate 130, fig. 1), overlapping the sacral vertebra dorsally.

The sacral "vertebra", the tenth of the series, is extremely peculiar, if not unique, consisting as it does of two separate bony halves joined



TEXT-FIG. 2—Modified Contour Reconstruction of Anterior Region of Urostyle, the Sacral Vertebra and part of the ninth Vertebra, posterior view. The most anterior section passes through the urostyle. Cartilage is indicated by dotted lines.

az10, anterior zygapophysis of tenth vertebra; fnar, fused neural arches; il, ilium; ivc, intervertebral cartilage; pz9, posterior zygapophysis of ninth vertebra; sd10, sacral diapophysis of tenth vertebra; sp11–13, eleventh to thirteenth spinal nerves; ur, urostyle

dorsally and ventrally by cartilage (Plate 130, fig. 1; Plate 131, figs. 7 and 9; Text-fig. 2). It is narrow antero-posteriorly compared with the other vertebrae. Essentially each bony half consists of a curved portion of the neural arch (representing the basidorsal), a prezygapophysis, and a sacral diapophysis attached to the middle of the basidorsal. The diapophysis, though much larger than those of the other vertebrae, is relatively unspecialised. It has a gradual and slight expansion distally and lies on top of the ilium, being bound to the latter by ligamentous tissue. Dorsally the two bony halves are united by a narrow strip of persistent cartilage forming the top of the neural arch, while ventrally they are joined by the continuous cartilage stretching between the centrum of the ninth vertebra and the urostyle. This cartilage may become calcified in late life, but in doing so always remains quite separate from the bony halves of the neural arch (Plate 130, fig. 1). In young frogs (i.e. during the first few months after hatching) cartilage occurs dorsally between the bony halves of the neural arch in all vertebrae, but this later ossifies in all except the sacral vertebra.

In *Ascaphus* (Noble, 1931), the sacral vertebra agrees with that of *Leiopelma* in the shape of the transverse processes, but is relatively wider from front to back and is figured as being entirely bony across the ventral surface. The dorsal surface is not shown. Here, again, further investigation would be useful to find if this is always the case. Evidence from X-rays gives no indication that the structure of the sacrum of *Ascaphus* agrees with that of *Leiopelma,* but the sacral vertebra is narrower than those preceding it.

In sections of frogs eight months to one year old, bone formation is already well advanced. As far as can be seen, the formation of "membrane bone arches" (Mookerjee) from connective tissue on either side of the basidorsals, and subsequent fusion of the original neural arch with these slightly increases the width of the arch. Ossification of the centra begins with the formation of perichondral layers of bone in the inner notochordal sheath. The intervening spaces above and below the notochord are then subject to enchondral ossification.

In development, the urostyle is quite clearly formed of a single hypochordal cartilage as Mookerjee (1930, 1931) has shown. To the anterior and dorsal portion of this cartilage are fused the postsacral vertebrae formed in development. Of these, usually not more than three occur. As a rule the neural arches of these vertebrae are fused together and enclose the end of the spinal canal (Plate 131, fig. 8). Almost invariably one finds a pair of small but unmistakable transverse processes on the first (and best developed) postsacral vertebra. A common condition of the anterior part of the urostyle is illustrated in Text-figure 2. The very small, posterior neural arch is open above, housing the extreme posterior part of the spinal canal. The latter is entered in front of the arch by the coccygeal nerve. The more anterior two arches are fused together dorsally, but allow the passage between them of the twelfth pair of spinal nerves. The most anterior arch bears small transverse processes and both the fused arches are joined medially to those of the opposite side by cartilage. The eleventh pair of nerves enter the spinal canal between the urostyle and the sacral arch.

Variations and Abnormalities

It is quite usual to find fusions of various kinds between successive vertebrae, the most usual places being between the fifth and sixth and between the atlas and the vertebra next behind it. One interesting abnormality that does occasionally occur is the presence of the sacral diapophyses on the ninth vertebra, leaving a postsacral vertebra quite free from the urostyle (Plate 131, fig. 6). The ninth vertebra in these unusual cases is found to be formed of two halves joined by cartilage dorsally and ventrally, but to have both pre- and postzygapophyses. The postsacral vertebra is fairly small and has backwardly directed transverse processes, but otherwise is quite normal. The vertebral column in front of the ninth vertebra is clearly normal. This forward displacement of the sacrum is by no means uncommon among Amphibia. Zaharesco (1935) has made statistical analyses of this condition (and also that of spinal nerve variation) in *Rana* and concludes that even in that genus one still finds an evolutionary trend towards the shortening of the presacral region of the vertebral column.

Spinal Nerves (Plate 130, fig. 2; Text-figs. 1 and 2)

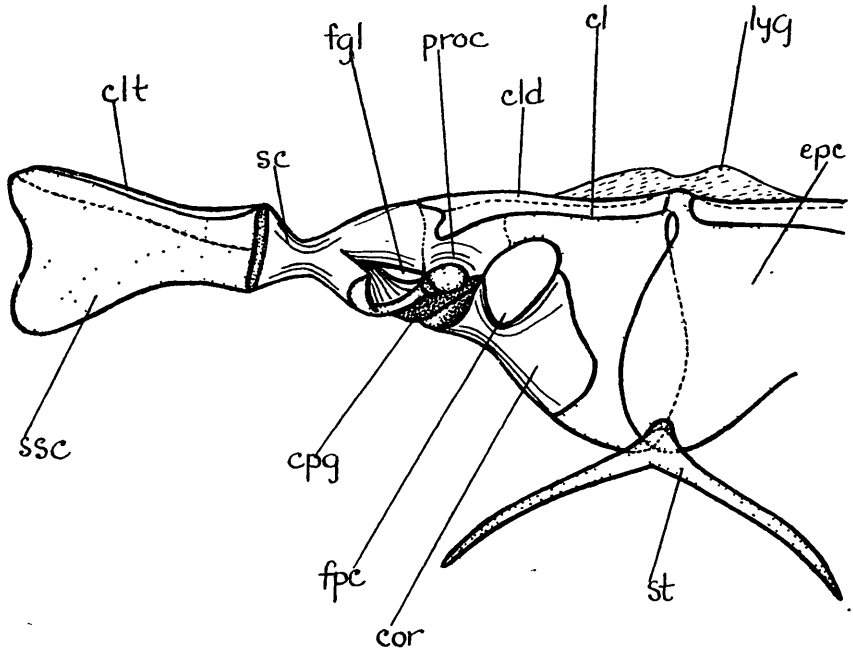
Normally, thirteen pairs of spinal nerves are present, all except the first having dorsal and ventral roots. A generalised diagram of their arrangement is given in Plate 130, fig. 2, but it must be emphasised that the brachial and sciatic plexuses are subject to a considerable degree of variation. The first spinal nerve, the N. suboccipitalis, has a ventral root only and passes out from the spinal canal in front of the neural arch of the atlas (Text-fig. 1 A and C), but not down between the occipital condyle and the atlas facet as figured by Mookerjee (1930, 1931) for *Triton* and *Bufo*. The presence of the N. suboccipitalis and its functional persistence throughout adult life must be regarded as an extremely primitive character. In Anurans it is usually transient, *Bufo* being an exception; in Urodeles it may persist for a time, but it is most unlikely that it ever becomes functional (Francis, 1934). In *Leiopelma*, it is always present in the adult, and becomes united with the N. hypoglossus at the point where the latter sends a branch nerve to the M. opercularis. It is clear that fibres from the N. suboccipitalis must pass to this muscle; in a few cases they can be seen to do so before its main trunk joins the N. hypoglossus. The position in early stages is clearer and the N. suboccipitalis can then be seen to send a separate branch to the muscle.

Large ganglia, corresponding to each nerve except the first, are developed outside the spinal canal. The tenth nerve in the series emerges between the ninth vertebra and the neural arch of the sacral vertebra, the eleventh behind the sacral arch. The twelfth nerve passes between the arches of the first and second fused vertebrae on the urostyle, the thirteenth (to which the N. coccygealis of *Rana* corresponds) between the second and third postsacral arches. The dorsal and ventral roots of this last slender nerve fuse within the spinal canal, so that it emerges as a single trunk.

The Pectoral Girdle (Text-fig. 3)

The pectoral girdle of *Leiopelma* has been described and graphically reconstructed by de Vos (1938 A). The reconstruction made, however,

is not entirely typical, and it has been thought advisable to make a further description and illustration of the girdle.



TEXT-FIG. 3—Pectoral Girdle, ventral view.

The girdle has been flattened so that all parts are seen in the same plane. The functionally dorsal surface of the suprascapula has now become ventral. The procoracoid is shown as if it were largely of bone, but actually it remains cartilaginous until fairly late maturity

cl, clavicle; cld, dorsal margin of clavicle; clt, cleithrum; cor, coracoid; cpg, cartilago paraglenoidalis; epc, epicoracoid; fpc, fenestra between procoracoid and coracoid; fgl, glenoid foramen; lyg, "lymph gland"; proc, procoracoid, sc, scapula, ssc, suprascapula; st, sternum

The pectoral girdle is arciferous, but the method of overlapping (left over right or vice versa) is variable. At their extreme anterior, the two epicoracoids join to form a single piece of cartilage which is embedded in a characteristic bilobed mass of lymphoidal tissue called by Noble (1931) the "lymph gland". Immediately surrounding the cartilage is a layer of dense fibrous connective tissue. Slightly further back the epicoracoids begin to separate, but for a short distance are joined ventrally by a narrow procartilaginous bridge. When overlapping begins, the latter gives way to fairly sparse fibrous tissue just sufficient to hold the two halves together.

The lateral extremity of the well-ossified coracoid on each side forms the postero-median boundary of the glenoid cavity. A strip of cartilage, the cartilago paraglenoidalis, separates the coracoid from the scapula. The latter, which encloses between its antero-median and postero-median divisions a glenoid foramen, reaches the clavicle anteromedially. Medially, also, it is adjacent to the procoracoid cartilage. The latter is very late in ossifying and in the few cases where ossification is at all definite it is restricted to the lateral region of the cartilage.

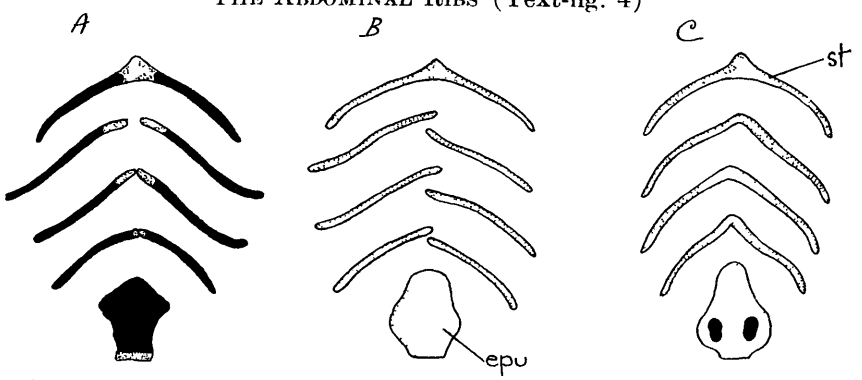
Laterally, it is united with the scapula, but the line of fusion between the two bones is generally visible. The procoracoid retains a double head of cartilage abutting on the glenoid cavity. The medial boundary of the procoracoid ossification is inclined to be irregular.

The clavicle has two divisions, each in the form of a flattened, bony strip. The ventral division is wider than the dorsal. The two parts are united anteriorly to form a groove into which the anterior rim of the procoracoid cartilage fits. De Vos states that the clavicle fuses laterally with the scapula, but I have not been able to confirm this.

The suprascapula usually becomes calcified, but a strip of uncalcified cartilage is left between the suprascapula and the bony scapula. Like the clavicle, the cleithrum is formed of two fused strips, and again the functionally dorsal division is the narrower. The suprascapula fits into the groove between the two strips of bone.

The sternum has two posterior styles as in *Bombina* (de Villiers, 1922). These may become fairly heavily calcified (Text-figure 4A), but always retain an uncalcified medial connection between each other. As de Vos has shown, the medial, anteriorly projecting piece of cartilage really consists of dorsal and ventral elements, the former lying embedded in the M. sternohyoideus, while the latter lies below the two epicoracoids at their posterior border.

THE ABDOMINAL RIBS (Text-fig. 4)



TEXT-FIG. 4—Sketches showing Variation in Abdominal Ribs and Epipubis
Calcified cartilage and bone are shaded black.
epu, epipubis; st, sternum

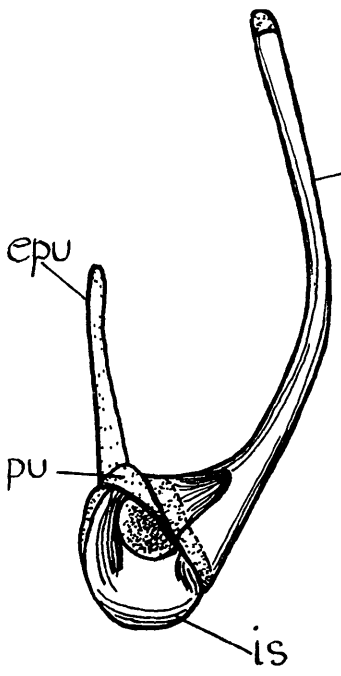
The so-called "abdominal ribs" of *Leiopelma* were first described and illustrated by Noble (1931). He referred to them as "large cartilages of much the same form as the abdominal ribs of the lizards, appearing in the myosepta of the M. rectus abdominis of *Leiopelma*." He was of the opinion that they have no ontogenetic or phylogenetic relationship to the true ribs and are dermal elements similar to the interclavicle in origin. In their adult condition they appeared to him to be remnants of the abdominal basket of Branchiosaurs and he realised that they are better developed in *Leiopelma* than in any urodele in which they occur.

De Vos (1938 B) investigated and reconstructed the abdominal ribs of an adult *Leiopelma* by means of microscopical sections. As a

result of a detailed study of the question she concluded that the inscriptional ribs represented not dermal elements, but cartilage bones similar to the ventral portions of true ribs in lizards. They thus cannot be included with the "ossa investitientia" (Gaupp) as can the sternal bones of primitive vertebrates (e.g. the abdominal ribs of *Sphenodon, Crocodilia, Archaeopteryx,* many fossil reptiles and certain Stegocephalia), "which do not pass through a cartilaginous stage, but ossify directly in the connective tissue of the cutis". Certainly, the inscriptional ribs of *Leiopelma* do have their earliest origins as strips of cartilage, and remain cartilaginous until fairly late maturity. They form a continuous series with the cartilaginous styles of the sternum. Some variations in the cartilages are shown in Text-fig. 4; e.g they may not reach each other, or they may overlap or fuse in the middle line. One mature *L. hochstetteri* prepared by means of the alizarin and toluidin blue method of Williams (1940) showed distinct alizarin staining in the cartilages (Text-figure 4 A). Obviously, then, the inscriptional ribs must become calcified or ossified in later life.

The Pelvic Girdle (Text-figure 5)

The most interesting feature of the pelvic girdle of *Leiopelma* is the presence of a cartilaginous, shield-shaped epipubis. A similar structure is possessed by *Ascaphus* (Noble, 1922, 1931; de Villiers, 1934), but the latter genus differs from *Leiopelma* by having also two posterior, subpelvic, skeletal rods which de Villiers has named the Nobelian bones and which are associated with the phallic organ. *Xenopus* is the only other Anuran genus apart from *Leiopelma* and *Ascaphus* to have an epipubis.



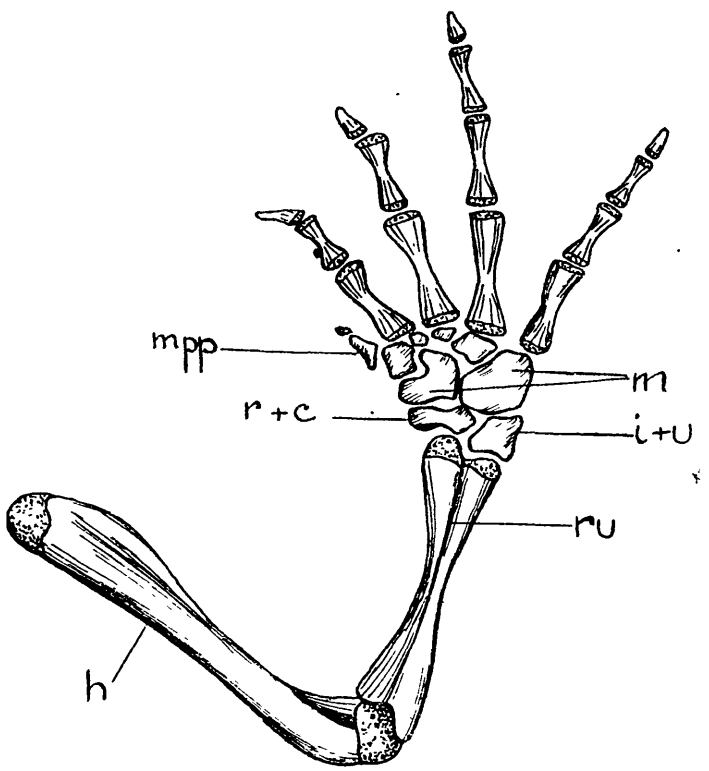
Text-fig. 5—Pelvic girdle, from the left side.
epu, epipubis; il, illum; is, ischium; pu, pubis

Although the epipubis of *Leiopelma* may, as de Villiers suggested, be a derivative of the linea alba which secondarily unites with the pubis, it has achieved complete continuity with the anterior ventral surface of the latter by the fourth week after hatching. It remains cartilaginous until maturity, but there is considerable evidence to show that in older specimens of *Leiopelma hochstetteri* at least it ultimately ossifies more or less completely. An epipubis in which two centres of ossification are present is shown in Text-figure 4 C, while Text-figure 4 A illustrates an epipubis which is almost completely ossified except for a posterior strip of cartilage. Frogs may be found in which the abdominal ribs are entirely cartilaginous, but the epipubis is mainly of bone. Like the abdominal ribs, the epipubis is partly

embedded in the M. rectus abdominis, but this muscle does not cover the cartilage ventrally. The pubis remains cartilaginous throughout life.

Carpus and Manus (Text-fig. 6)

In addition to the usual Anuran phalangeal formula of 2,2,3,3, a small phalangeal element can be found distal to the metacarpal of the prepollex. The free adult carpal elements number eight, but the number and position of fusions taking place during development is not com-



Text-fig. 6—Forelimb and Carpus of *L. hochstetteri*
h, humerus; i + u, intermedium + centrale; m, medialia; mpp, metacarpal of prepollex; ru, radio-ulna

pletely known. The naming of the adult carpal elements in Text-fig. 6 is therefore incomplete and provisional.

Leiopelma agrees in number of carpal elements and the possession of a phalangeal remnant on the prepollex with *Bombina bombina* (Ridewood and Howes, 1888). *Ascaphus*, according to Gregory, Miner and Noble (1923) has seven free carpal elements. X-ray photographs of *Ascaphus*, however, seem to indicate the possession of eight free

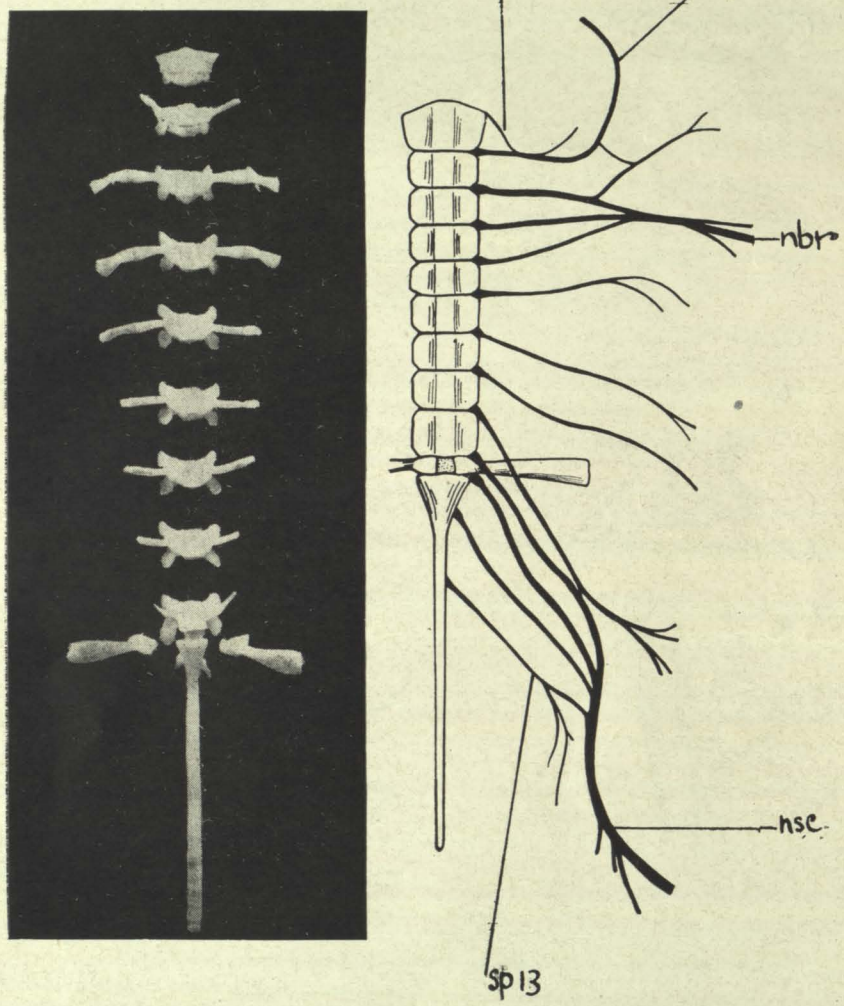


FIG. 1—Photograph of disarticulated adult vertebral column, ventral view.

FIG. 2—Generalised diagram of the spinal nerves and vertebrae.

nbr, N. brachialis; nsc, N. ischiadicus (sciatic nerve); spl, N. spinalis 1 (N. suboccipitalis); sp2, N. spinalis 2 (N. hypoglossus); sp3, N. spinalis 13 (N. coccygeus).

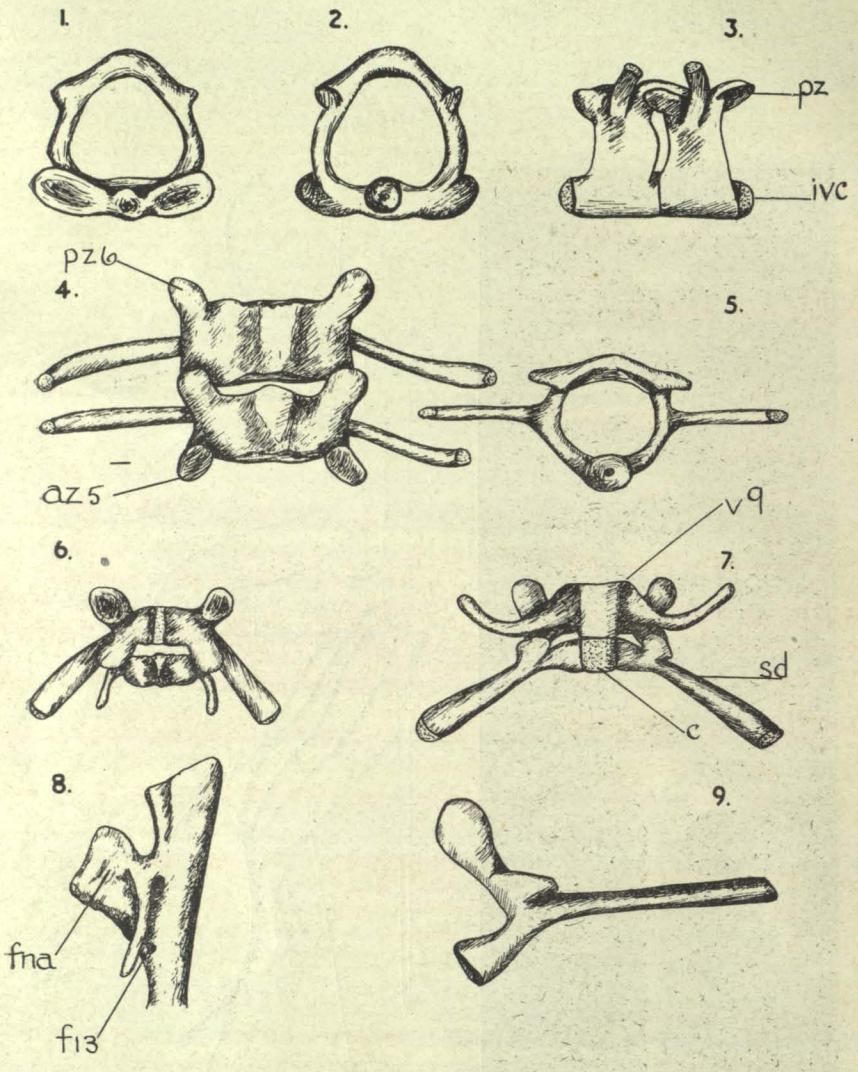


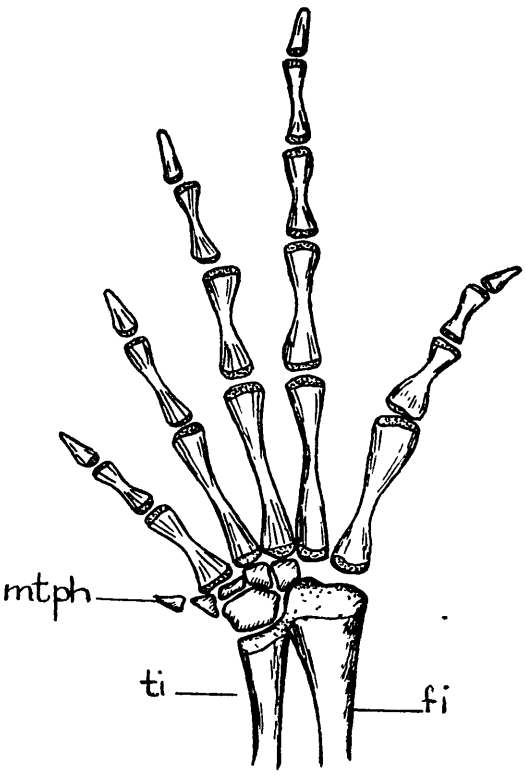
FIG. 1—Atlas vertebra, anterior view. FIG. 2—Atlas vertebra, posterior view. FIG. 3—Two trunk vertebrae, lateral view. FIG. 4—Fifth and sixth presacral vertebrae, dorsal view. FIG. 5—Fifth presacral vertebra. anterior view. FIG. 6—Abnormal sacrum, dorsal view. The sacral diapophyses are attached to the ninth vertebra and the small tenth vertebra is postsacral. FIG. 7—Normal sacrum, ventral view. FIG. 8—Anterior of urostyle, lateral view. FIG. 9—Left half of sacral vertebra, anterior view. The magnifications vary.

az5, prezygapophysis of fifth vertebra; c, cartilage; fna, fused neural arches; f13, foramen for 13th spinal nerve; ivc, intervertebral cartilage; pz, postzygapophysis; pz6, postzygapophysis of sixth vertebra; sd,, sacral diapophysis; v9, ninth presacral vertebra.

bony elements and it is possible that the carpus of this genus would repay further investigation. No indication of a phalanx on the prepollex has yet been found in *Ascaphus*. If *Ascaphus* really has eight free carpal elements, it joins *Leiopelma* and *Bombina* in the possession of a more primitive carpal pattern than is presented by any other Anuran.

TARSUS AND PES
(Text-fig. 7)

The phalangeal formula is 2,2,3,4,3, and the prehallux is represented by a small, usually cartilaginous metatarsal. As in *Bombina bombina,* five free tarsal elements occur in addition to the tibiale and fibulare. I can find no record of a description of the tarsus of *Ascaphus*. An X-ray photograph shows at least four and probably five separate bones.



TEXT-FIG. 7—Tarsus and Pes of *L. hochstetteri*
ti, tibiale (astragalus) fi, fibulare (calcaneum)
mtph, metatarsal of prehallux

SUMMARY OF THE SKELETAL CHARACTERS OF *Leiopelma*

*1. All vertebrae are amphicoelous.
*2. Nine presacral vertebrae occur.
3. The neural spines are not sharply defined.
†*4. The "atlas" vertebra lacks transverse processes.
*5. Ribs are present in association with the third and fourth vertebrae and occasionally also with the fifth. Characteristic processes are developed on the ribs.
*6. The sacral diapophyses are simple and relatively unexpanded.
7 The sacral vertebra is typically narrower than the others and is formed of two separate bony halves joined dorsally and ventrally by cartilage.
8. During development the urostyle is formed of a single hypochordal cartilage to which up to three postsacral vertebrae become fused.
9. Fusions between successive vertebrae are not uncommon, especially between the first and second, and the fifth and sixth.
10. The sacrum may occasionally be forwardly displaced to the ninth vertebra, thus producing a small postsacral vertebra, distinct from the urostyle.

11. Thirteen pairs of spinal nerves are usually present.
12. The first spinal nerve is the N. suboccipitalis, which has a ventral root only. Some fibres from this nerve pass to the M. opercularis.
*13. The pectoral girdle is arciferous, but the epicoracoids are united at their anterior tips.
14. Overlapping of the epicoracoids may be left over right or vice versa.
*15. The procoracoid may show partial ossification.
*16. A cartilago paraglenoidalis separates the coracoid from the scapula.
*17. A cleithrum is present.
18. The sternum has two posterior styles.
19. Abdominal ribs, which originate as cartilaginous strips, are present in the M. rectus abdominis and form a continuous series with the styles of the sternum.
*20. A cartilaginous, shield-shaped epipubis is present. It may ossify in late maturity.
21. Nobelian bones are absent.
22. The pubis remains cartilaginous throughout life.
23. A small phalangeal element lies distal to the metacarpal of the prepollex.
†*24. The free adult carpal elements number eight.
25. The prehallux is represented by a small metatarsal.
†*26. Five free adult tarsal elements occur in addition to the tibiale and fibulare.

* Characters in which *Ascaphus* is known to agree with *Leiopelma*.

† Characters in which *Ascaphus* may be considered to agree with *Leiopelma*, although the evidence is not conclusive.

Skeletal Characters in which *Ascaphus* is Known to Differ from *Leiopelma*

1. The structure of the sacral vertebra. (But this point possibly needs further investigation in *Ascaphus*.)
2. The shape of the sternum. In *Ascaphus* it is narrow anteroposteriorly and wide laterally and has no long styles.
3. The absence of abdominal ribs in *Ascaphus*.
4. The presence of Nobelian bones in the male *Ascaphus*.

General Summary

The vertebral column, appendicular skeleton and spinal nerves of *Leiopelma hochstetteri* Fitzinger are described. Where possible, comparison is made with *Ascaphus truei* and with members of the Discoglossidae.

Leiopelma shows many skeletal features which may be regarded as primitive. These include the possession of nine presacral amphicoelous vertebrae; at least two pairs of true ribs; simple and only slightly expanded sacral diapophyses; up to three postsacral vertebrae

fused to the hypochordal element of the urostyle; thirteen pairs of spinal nerves, of which the most anterior nerve is the N. suboccipitalis; an arciferous pectoral girdle; a cleithrum; abdominal ribs; an epipubis; a persistently cartilaginous pubis; a phalanx on the metacarpal of the prepollex; eight free adult carpal elements and five free adult tarsal elements.

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